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Population Characteristics and Food Resource Utilization of *Conus* in the Galapagos Islands[1]

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ABSTRACT: Two large collections of *Conus* from the Galapagos Islands permitted the analysis of size, sex ratio, and food of 4 of the estimated 13 species of *Conus* present in the islands. The species investigated were *C. diadema*, *C. lucidus*, *C. tiaratus*, and *C. nux*. Significantly unequal sex ratios were found in the samples of *C. diadema*, *C. lucidus*, and *C. tiaratus*, but there was no indication of sexual dimorphism in shell sizes. *Conus diadema* was found to have the most catholic diet of the species, consuming mainly polychaetes of the family Terebellidae, but also sipunculids, mollusks, and eight other polychaete families. Very few food items were recovered from the guts of *C. lucidus* and most were polychaetes of the families Sabellariidae and Capitellidae. *Conus tiaratus* and *C. nux* were both found to feed primarily on polychaetes of the families Nereidae and Eunicidae. In both cases, the dominant species was *Nereis jacksoni*. Comparison of diets between cognate species in the Galapagos and the Indo-West Pacific indicated the Galapagos species consumed somewhat different prey species. Although there are significantly fewer *Conus* species per habitat in the Galapagos than in the Indo-West Pacific, there were no significant differences with respect to number of prey species consumed or prey species diversity between the areas. Thus, there was no evidence of decreased dietary specialization in the presence of fewer competing congeners.

THE GALAPAGOS ISLANDS and their fauna have elicited considerable interest from biologists since the famous visit of Darwin in 1835. However, most of this interest has been directed at the terrestrial fauna and to the unique assemblage of marine vertebrates such as penguins, cormorants, and lizards. Relatively little attention has been paid to the marine invertebrate fauna. Most studies on the marine invertebrate fauna of the islands have been taxonomic or zoogeographic (Bowman 1966) and have generally shown that the marine invertebrate fauna is most closely related to that of the East Pacific and Caribbean (Abbott 1966) rather than the richer Indo-West Pacific.

The Galapagos, together with Clipperton and Isla Rivelligegados, represent the most isolated outposts of the East Pacific *Conus* species. They are further of interest in that the marine environment is considered to be warm temperate (Abbott 1966) rather than tropical, which is the climate most other *Conus* assemblages exist under in the East Pacific area. It is thus of some interest to compare the ecology of *Conus* species assemblages on these islands with similar sets from tropical regions to see if the lack of tropical conditions and the isolated nature of the islands have affected the ecological characteristics of the assemblages. It is the purpose of this paper to begin such an ecological analysis by considering the food and population characteristics of the more common Galapagos species.

The specimens upon which this paper is based were collected by J. J. Von Mol of the University of Brussels, Belgium, in 1970 and by G. M. Wellington of the University of California at Santa Barbara in 1973 and 1974. I am greatly indebted to them for placing this material at my disposal.

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MATERIALS AND METHODS

All specimens were collected by hand at low tide, by diving, or by dredging from a small vessel. Most specimens were boiled for a few minutes to stop enzyme action in the gut and then preserved in 70 percent ethanol. The shell of each individual was measured with a vernier caliper to the nearest 0.1 mm. The measurements recorded were maximum length and greatest width. Following measurement, each shell was cracked open and the animal extracted and sexed. The digestive tract was then opened under a dissecting microscope and any contents were removed and mounted on a microscope slide. The slides were later analyzed to determine the prey species ingested. Since all species reported here consumed primarily polychaete worms, the gut contents were jaws and setae. These were identified using standard references (Day 1967, Fauchald 1968, 1970, Hartman 1940, 1944, 1947, 1950). Initial identifications were verified by Kristian Fauchald of the University of Southern California, to whom I am most grateful. Prey diversity calculations were made using the Shannon-Weaver index (Pielou 1966).

RESULTS

Species Composition of the Conus Fauna

Of the 30 or so species of *Conus* that are known from the East Pacific zoogeographical realm (Keen 1971, Nybakken 1970), relatively few appear to be present in the Galapagos. An analysis of the Panamic *Conus* species present in the Galapagos as reported in the literature and as derived from the present material is given in Table 1. From this table, it can be seen that 13 species have been reported from the Galapagos. Of these, *C. chaldeus* and *C. ebraeus* are immigrants from the Indo-West Pacific, where they are common species (Kohn 1959, 1968, Kohn and Nybakken 1975). This leaves 11 species that would appear to be indigenous inhabitants of these islands. Of these, 10 species were represented in the samples that form the basis for this paper: *C. brunneus*, *C. dalli*, *C. diadema*, *C. fergusoni*, *C. gladiator*, *C. lucidus*, *C. nux*, *C. purpurascens*, *C. tiaratus*, and *C. ximenes*. Four species, *C. diadema*, *C. lucidus*, *C. nux*, and *C. tiaratus*, were present in sufficient numbers to enable food analysis to be performed (Table 2).

It is of interest to note that the Galapagos *Conus* fauna appears to be depauperate when compared to the mainland coast. It seems that only 13 species occur throughout the islands. I lack good data for selected sampling spots on the southern Central American coast, but even as far north as Guaymas, Mexico, near the outer limits of the Panamic *Conus* fauna, 19 species are reported (DuShane and Poorman 1967). Also, certain of the more common mainland species appear to be completely absent from the Galapagos. Notable in this regard are *C. princeps* and *C. regularis*. Why this should be true is not clear, but it may be related to reproductive strategies or may simply represent inadequate sampling of the islands. An interesting ecological question is whether the food or habitat niches of these usually dominant species have been occupied by other species.

In terms of relative abundance, in these samples at least, it would appear that *C. lucidus*, *C. diadema*, and *C. tiaratus* are the most abundant (Table 2), with *C. nux* being considerably less abundant than along the mainland coast (Nybakken, in press). The remainder of the species are rare, at least in these samples, but it is not known whether this is also reflected in the natural habitat.

Size and Sex Ratio

Information on size and sex ratio was obtained for only the four most abundant species, *C. diadema*, *C. lucidus*, *C. nux*, and *C. tiaratus*. The size frequency distributions are given in Figure 1.

With the exception of *C. nux*, the sex ratio in the samples was significantly different from 50:50 (χ^2 test, $P < 0.05$). In the cases of *C. diadema* and *C. tiaratus*, the males were more abundant almost by a factor of two. In *C. lucidus*, the females were more abundant, again by a factor of about two. This would

TABLE 1

Conus SPECIES REPORTED FROM THE GALAPAGOS ISLANDS

SPECIES	HANNA (1963)	DALL (1910)	KEEN 2ND ED (1971)	EMERSON AND OLD (1962)	WELLINGTON SAMPLE, THIS STUDY	VON MOL SAMPLE, THIS STUDY
C. archon						
C. arcuatus						
C. bartschi						
C. brunneus	×	×		×	×	
C. californicus						
C. chaldeus			×			
C. dalli	×		×	×	×	
C. diadema	×		×	×	×	×
C. dispar						
C. ebraeus	×		×			
C. emersoni						
C. fergusoni	×	×	×	×	×	×
C. gladiator		×	×	×	×	
C. gradatus						
C. lucidus	×	×			×	×
C. nux	×	×		×	×	×
C. orion						
C. patricius		×				
C. perplexus						
C. princeps						
C. purpurascens	×	×		×	×	×
C. recurvus						
C. regularis						
C. scalaris						
C. tessulatus						
C. tiaratus	×	×			×	×
C. tornatus						
C. virgatus						
C. vittatus						
C. ximenes	×					×

TABLE 2

RELATIVE ABUNDANCE OF *Conus* IN TWO SAMPLES FROM THE GALAPAGOS ISLANDS

SPECIES	VON MOL SAMPLE	WELLINGTON SAMPLE	TOTAL NUMBER OF SPECIMENS	NUMBER USED IN FOOD AND POPULATION STUDY*
C. brunneus	1	1	2	1
C. dalli	0	4	4	0
C. diadema	55	57	112	99
C. fergusoni	5	7	12	0
C. gladiator	0	1	1	1
C. lucidus	163	12	175	117
C. nux	20	24	44	38
C. purpurascens	1	1	2	0
C. tiaratus	70	27	97	87
C. ximenes	10	0	10	0
Total			460	343

*Some specimens were not boiled and hence could not be used in the food analysis. Others were received without shells or were dried and similarly could not be used in the food or population analysis; hence, the discrepancy between this column and the one listing the total number of specimens available.

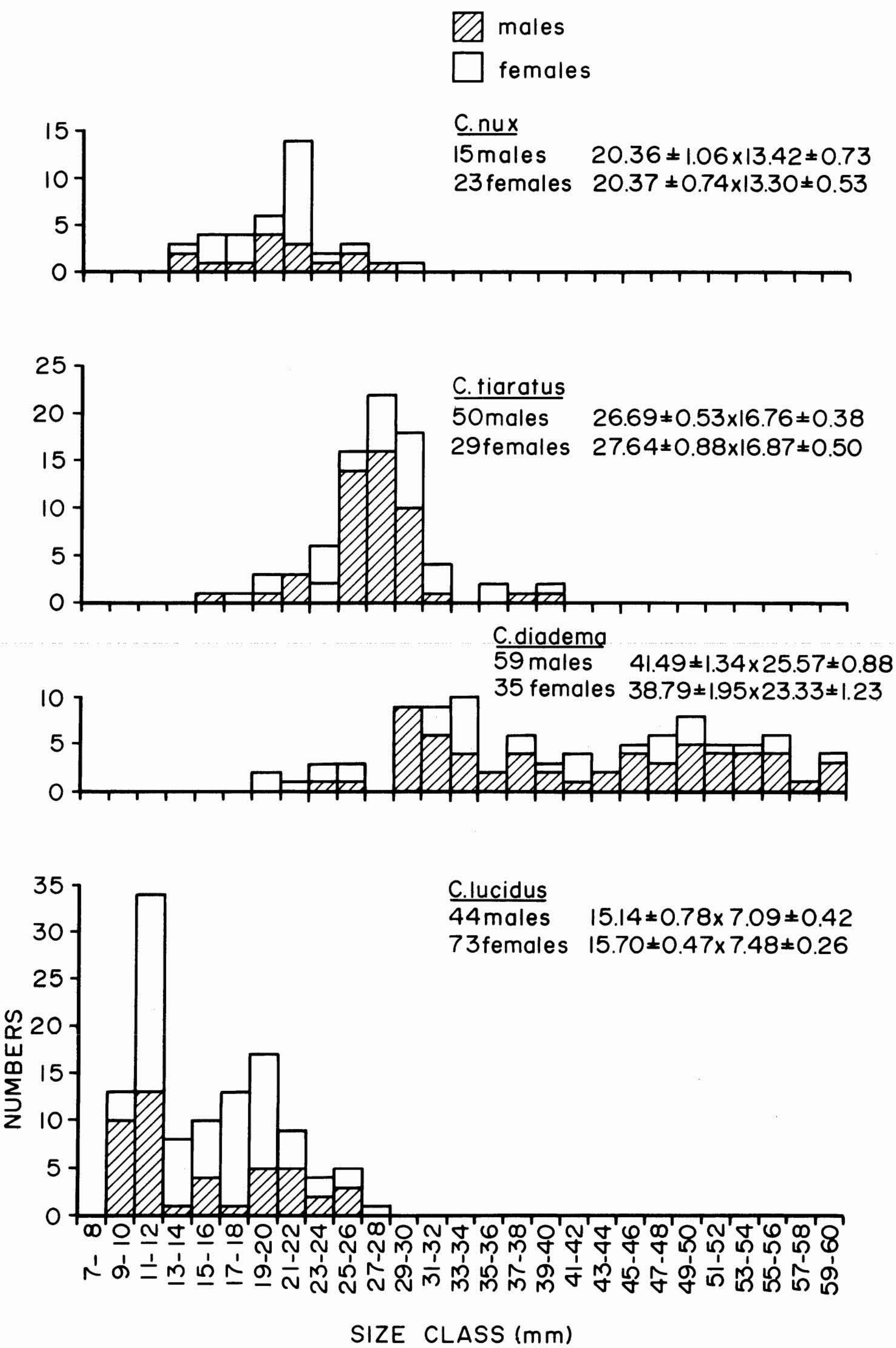

FIGURE 1. Length and sex frequency distributions of the four *Conus* species abundant in the Galapagos. Sample size, mean shell length, and mean maximum shell width plus or minus the standard error of the mean are given for both sexes.

TABLE 3

FOOD OF THE FOUR DOMINANT SPECIES IN THE GALAPAGOS

PREY SPECIES	*C. diadema*	*C. lucidus*	*C. tiaratus*	*C. nux*	TOTALS
Thelepinae sp. A	17			1	
Eupolymnia sp.	7				
Terebella sp.	3				
Polycirrus sp.	2				
Sabellinae		1			
Ampharete sp.	1	1			
Lygadamis sp.		3			
Sabellariidae		1			
Stenelanella sp.	1	1			
Chaetozone sp.	1				
Cirriformia sp.	1				
Cirratulidae	1				
Eurythoe sp.	5				
Phyllodocidae	3				
Polynoidae	1			3	
Capitellidae		3	1		
Sipunculid	3				
Gastropod mollusk	2				
Syllidae	1			2	
Nereis jacksoni	1		55	9	
Neanthes sp. C			10	9	
Neanthes sp. D			1		
Ceratonereis sp.		1			
Unknown nereid		1	7	2	
Eunice afra			3		
Eunice biannulata			3		
Arabella mutans			1		
Lumbrinereis sp.			4	1	
Onuphinae			4		
Unknown eunicid			3		
Unidentified	1		1		
Number examined	99	117	87	38	341
Total food items	50	12	93	27	182
Percentage with food in gut	51	10	62	55	
Prey diversity, H'	2.26	1.94	1.50	1.61	
Evenness, J'	0.82	0.93	0.63	0.82	
Niche breadth, $1/B$	6.16	6.00	2.67	4.03	
Number of prey species	16	8	12	7	
Number with food	50	12	54	21	

seem to be a very high deviation from unity, considering the small number of species considered. Unequal sex ratios are seemingly much rarer among the Indo-Pacific *Conus*, having been reported only for *C. ebraeus* (Kohn 1968) and *C. sanguinolentus* (Marsh 1971).

There were no significant differences between males and females as to length or width among the four common species (t test, $P > 0.05$).

Food and Feeding

Of the 341 specimens examined of the four most abundant species, 137 were found to have remains of prey items in their alimentary canals. The prey items in all four species were predominantly polychaete worms. Table 3 lists the main prey organisms and pertinent statistics for the four most abundant species, *C. diadema*, *C. lucidus*, *C. tiaratus*, and *C. nux*.

TABLE 4

NUMBER OF *Conus* SPECIES PER HABITAT, NUMBER OF SPECIES CONSUMED, AND PREY SPECIES DIVERSITY FOR SEVERAL GEOGRAPHIC AREAS

CATEGORY	GALAPAGOS*	HAWAII BENCH (Kohn 1966, 1971)	HAWAII REEF (Kohn 1966, 1971)	INDONESIA (Kohn and Nybakken 1975)	MALDIVES (Kohn 1968)	CHAGOS (Kohn 1968)
Range of *Conus* species/habitat	2–5	6–9	7–10	6–27	9–19	8–12
Mean number of *Conus* species/habitat	3.23±0.42	7.75±0.63	9.0±0.71	14.1±2.34	13±2.2	10
Range of prey species diversity	1.5–2.26	0.22–1.94	0.7–1.24	0.5–2.1	0.29–2.19	0.63–1.84
Mean prey species diversity	1.83±0.17	1.11±0.46	1.25±0.2	1.37±0.2	1.15±0.33	1.16±0.22
Range of number of prey species eaten	7–16	2–11	3–10	2–15	3–13	2–10
Mean number of prey species eaten	10.8±2.0	6.3±2.5	6.8±1.5	7.4±1.3	6.3±1.7	5.2±1.3

NOTE: Means are given with standard errors.
* Galapagos data for number per habitat from Wellington sample only.

Conus diadema had the most catholic diet of the four species. Although remains of the polychaete family Terrebellidae dominated the gut contents, it also fed upon members of eight other polychaete families and such diverse phyla as sipunculids and mollusks (Table 3). This great diet diversity is reflected in the high prey diversity index value (H') of 2.26.

Conus lucidus was the most abundant species in terms of the numbers of individuals dissected, but few individuals had prey remains in the gut. Since only 12 food items were recovered, it is difficult to generalize about the diet of this species. The few results, however, indicate that sedentary polychaetes of the families Sabellariidae and Capitellidae were consumed most. A larger sample would be warranted here to resolve diet preferences. Although accurate and detailed substrate data are generally unavailable for these samples, the notes accompanying certain samples indicate that this species was taken primarily on sand, where the other three abundant species were seldom found.

Conus tiaratus yielded the greatest number of food items (93) and had the highest percentage with food in the alimentary canal (62 percent). *Nereis jacksoni* constituted 59 percent of the diet, and almost all prey items were from the polychaete families Nereidae and Eunicidae (Table 3). Whereas *C. diadema* and *C. lucidus* had but single prey items in their digestive tracts, *C. tiaratus* most often had consumed several individuals. This is reflected in the relatively high average number of prey items per animal of 1.7.

Although *C. nux* is extremely abundant in mainland samples, it was present in the fewest numbers among the four abundant species in these Galapagos samples. Of the 38 specimens dissected, 21 had food in the digestive tract. The dominant prey items were *Nereis jacksoni* and an unknown species of *Neanthes* (Table 3). As in *C. tiaratus*, multiple ingestions were common, resulting in an average number of prey items per animal of 1.3.

The specimens of *C. brunneus* and *C. gladiator* did not yield any prey items. The few specimens of *C. ximenes*, *C. fergusoni*, *C. dalli*, and *C. purpurascens* were not boiled and hence were not dissected for food.

DISCUSSION

The diets of four species of *Conus* from the Galapagos Islands are described herein for the first time. All were found to be primarily vermivorous, as are the common species of the Indo-Pacific. Kohn (1966) has shown that, where large numbers of *Conus* species co-occur in the Indo-Pacific, the diet is more specialized than when only a single species occurs. This suggests a more general observation that as the number of competing *Conus* species per habitat decreases, the diet becomes less specialized. If this observation can be shown to be true, it is consistent with the hypothesis that interspecific competition is important in structuring *Conus* assemblages. Kohn (1966) unfortunately deals only with a comparison between a habitat with one *Conus* species and a habitat with between six and nine species. An intermediate habitat was not compared. The present data now allow such a comparison to be made if we can assume that the current samples are reflective of thorough habitat sampling in each of the areas collected and hence are representative of relative abundance. I assume here that such is the case.

I have noted that only 13 species of *Conus* are reported from the Galapagos, but this is a figure for the whole archipelago. The average number of *Conus* species per habitat for the islands has been computed from the current data; this figure is 3.23 ± 0.42, or considerably fewer than the total.

Table 4 lists the pertinent parameters of number of *Conus* species per habitat, prey species diversity, and number of prey species eaten for the current data from the Galapagos and several other sample areas in the Indo-Pacific. Table 5 gives the results of analysis of variance tests among these parameters for the Galapagos and four other sampling areas in the Indo-Pacific. It is important to note here that in all cases, there are significantly fewer *Conus* species per habitat in the Galapagos compared to other Indo-Pacific areas. At the same time, however, there are no significant differences between the Galapagos and the other areas with respect to number of prey species consumed and prey species diversity. It would thus appear that there is no evidence of decreased dietary specialization in the presence of fewer competing congeners. Unfortunately, the absence of any data on abundance of prey species in the substrate does not allow another important comparison to be made—namely, whether there are similar arrays of prey species to exploit in the Galapagos and Indo-Pacific. It is thus possible that the absence of significant differences in specialization may be due to a lesser array of prey species available in the substrate.

TABLE 5

ANALYSIS OF VARIANCE TABLES COMPARING THE GALAPAGOS *Conus* ASSEMBLAGE WITH FOUR AREAS IN THE INDO-PACIFIC (HAWAII BENCH, HAWAII REEF, INDONESIA, AND THE MALDIVES)

A. NUMBER OF SPECIES OF *Conus* PER HABITAT

	SS	d.f.	MS	*F*	*P*
Treatment	507.37	3	126.8	7.5	<0.01
Error	303.50	18	16.9		
Total	810.87	22			

B. NUMBER OF PREY SPECIES CONSUMED

	SS	d.f.	MS	*F*	*P*
Treatment	69.00	4	17.25	0.88	>0.1
Error	565.70	29	19.51		
Total	634.70	33			

C. PREY SPECIES DIVERSITY

	SS	d.f.	MS	*F*	*P*
Treatment	1.77	4	0.44	0.87	>0.1
Error	13.68	27	0.51		
Total	15.45	31			

TABLE 6

COMPARISON OF FOODS OF COGNATE SPECIES IN THE INDO-PACIFIC AND THE GALAPAGOS

PREY GROUP	*C. lividus**	*C. diadema*	*C. miliaris**	*C. tiaratus*
Platynereis	13			
Nereis		1		55
Neanthes				10
Nereidae			3	8
Eunice			12	6
Lysidice			62	
Nematonereis			2	
Palola			11	
Lumbrinereis				4
Onuphinae				4
Arabella				1
Eunicidae				3
Lepidonotinae	1	1		
Phyllodocidae	2	3		
Eurythoe		5		
Terebellidae	22			
Thelepinae		17		
Thelepus	2			
Euthelepus	2			
Eupolymnia		7		
Polycirrus	5	2		
Loimia	14			
Nicolea	17			
Terebella	1	3		
Axiothella	15			
Maldanidae	10		1	
Capitellidae			1	1
Ampharetidae		1		
Cirratulidae	4	1		
Cirriformia	6	1		
Lygadamis	2			
Sabellastarte	3			
Ptychodera	65			
Stenelanella		1		
Chaetozone		1		
Syllidae		1	1	
Gastropod mollusk		2		
Sipunculida		3		

*Data for Indo-Pacific from Kohn (1959, 1968), Kohn and Nybakken (1975), and Marsh (1971).

Finally, it is of some interest to compare the food in cognate *Conus* species between the Indo-Pacific and the Galapagos. Based on shell morphology and radula characteristics, *C. diadema* and *C. lividus* are closely related, as are *C. miliaris* and *C. tiaratus*. *Conus nux* seems most closely related to *C. sponsalis* of the Indo-Pacific. No close cognate of *C. lucidus* in the Indo-Pacific is known to me at present. Of the above three cognate species pairs, adequate food data are available only for *C. diadema* and *C. lividus*, and *C. miliaris* and *C. tiaratus*. Comparisons of food items between these pairs are given in Table 6. I compared food on the basis of genera rather than species, because in most cases, exactly similar species are not present in both areas.

In the case of *C. diadema* and *C. lividus*, the correspondence in diet is similar in that both tend to feed on terebellid polychaetes. The major difference appears to be that *C.*

lividus preys significantly on the enteropneust *Ptychodera*, but *C. diadema* does not. On the other hand, *C. diadema* eats sipunculids and mollusks—items not found in the diet of *C. lividus*. With *C. miliaris* and *C. tiaratus*, the differences are more pronounced. *Conus miliaris* eats primarily eunicids, whereas *C. tiaratus* has a diet predominantly of nereids. Again, lack of prey availability data does not permit us to determine whether these differences are due to different prey abundance or availability patterns in the two areas.

Finally, it must be noted that the samples upon which the above discussion and comparisons were made are relatively small and a real possibility exists that the samples and/or sampling are inadequate to assess the within-habitat diversity and abundance of *Conus* in the Galapagos. Perhaps, this paper will stimulate further sampling.

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